# Estimation of Neuronal Dynamics of Izhikevich Neuron Models from Spike-Train Data with Particle Markov Chain Monte Carlo Method

Inoue, Hiroaki

Hukushima, Koji

Omori, Toshiaki

(Citation)
Journal of the Physical Society of Japan,90(10):104801

(Issue Date)
2021-10-15

(Resource Type)
journal article

(Version)
Version of Record

Journal of the Physical Society of Japan **90**, 104801 (2021)
https://doi.org/10.7566/JPSJ.90.104801

# Estimation of Neuronal Dynamics of Izhikevich Neuron Models from Spike-Train Data with Particle Markov Chain Monte Carlo Method

Hiroaki Inoue[1], Koji Hukushima[2,3], and Toshiaki Omori[1,4*]

[1]*Department of Electrical and Electronic Engineering, Graduate School of Engineering, Kobe University, Kobe 657-8501, Japan*
[2]*Graduate School of Arts and Sciences, The University of Tokyo, Meguro, Tokyo 153-8902, Japan*
[3]*Komaba Institute for Science, The University of Tokyo, Meguro, Tokyo 153-8902, Japan*
[4]*Organization for Advanced and Integrated Research, Kobe University, Kobe 657-8501, Japan*

(Received April 21, 2021; accepted August 3, 2021; published online September 10, 2021)

Many neuronal models reproducing electrical activities of neurons have been proposed. Among such neuronal models, the Izhikevich neuron model is known to reproduce various kinds of electrical responses with low computational cost. It is difficult, however, to determine the model parameters of neuronal models including the Izhikevich neuron model which reproduce observed data since the latent variables of the neurons, such as membrane potential and channel variables, cannot be observed directly and only one of multidimensional latent variables of neurons or only spike-train data can be observed through partial observations. In this paper, we propose a data-driven method for estimating the latent variables and the parameters of the Izhikevich neuron model from only spike-train data. In the proposed method, we estimate the joint posterior distribution of latent variables and parameters by employing the replica exchange particle-Gibbs with ancestor sampling method, in order to overcome existence of local optima in parameters due to limited observations. Furthermore, we verify the effectiveness of the proposed method by using spike-train data generated from the Izhikevich neuron model.

## 1. Introduction

Elucidating neuronal dynamics is one of the important subjects to reveal information processing in neural systems. For this purpose, it is necessary to establish a data-driven method for estimating neuronal dynamics from spike-train data. Each neuron in neural systems is known to have various electrical characteristics, such as tonic, phasic, and rebound spikings, and many kinds of neuronal models have been proposed for expressing a part of such electrical responses of the neurons.[1–10] The Izhikevich neuron model, one of neuronal models, is known to reproduce various kinds of electrical responses with low computational cost.[9,10] However, it is difficult to determine the model parameters that reproduce the electrical responses of neurons since the latent variables of the neurons such as membrane potential and channel variables cannot be observed directly and only one of multidimensional latent variables of neurons or only spike-train data can be observed through partial observations.

In order to estimate neuronal dynamics based on data-driven approaches, methods based on the maximum likelihood (ML) method have been proposed.[11–14] However, previous studies based on the ML method[11–14] assumed that we can observe a continuous latent variable such as membrane potential or florescence of calcium imaging rather than spike-train. A previous study proposed an ML method for estimating leaky integrate-and-fire neuron based on spike-train data.[15] However, the kind of neuronal response is limited to tonic spiking and estimated results would be a local optimum. Moreover, other study proposed a method for estimating the Hodgkin–Huxley model[1] based on spike-train data.[16] In this method, the process of obtaining spikes is formulated as the state space model[11–14,17–34] based on the Hodgkin–Huxley neuron model, and the membrane potentials, which are the latent variables of the neuron, are estimated from spike-train data by using the sequential Monte Carlo (SMC) method.[11–14,18,20,22,24,25,27–31,34] The parameters in the model are also estimated simultaneously by the SMC method with the self-organizing state space model (SOSSM),[20] that the parameters are assumed as the latent variables that do not change over time. However, this method requires that the range of possible values of the parameters be known in advance. Moreover, the accuracy of this method is strongly affected by the problem of the degeneracy in the SMC method.

A method that combines the SMC method and the expectation–maximization (EM) algorithm[24,35,36] has been proposed for estimating the parameters of state space models.[11–14,31] This method is a method of sequentially updating the parameters so that the likelihood increases, and it is guaranteed that a local optimum can be estimated. However, this method is highly dependent on the initial values of the parameters used in the estimation, and there is a possibility that a global optimum cannot be estimated. The particle-Gibbs (PG) method has been proposed to estimate latent variables and parameters of state-space models simultaneously.[25,27,29,30,34] It is possible to obtain samples from the joint posterior distribution of latent variables and parameters by employing the SMC method in Gibbs sampling.[24,37] The PG method is one of the particle Markov chain Monte Carlo (PMCMC) methods,[25,27–30,34] and it is guaranteed that the joint posterior distribution can be estimated by obtaining an infinite number of samples. Moreover, in recent years, the replica exchange particle-Gibbs with ancestor sampling (REPGAS) method has been proposed to improve the sampling efficiency by combining the replica exchange method[38–40] with the PG method.[34]

In this paper, we propose a data-driven method based on REPGAS for estimating the joint posterior distribution of latent variables and parameters in the Izhikevich neuron model from only spike-train data. In this study, we assume that only spike-train data are observable due to partial observations, while most of previous works assumed either direct measurements of membrane potentials or imaging measurements of membrane responses.[11–14] We realize the estimation of the global optimum for the Izhikevich neuron

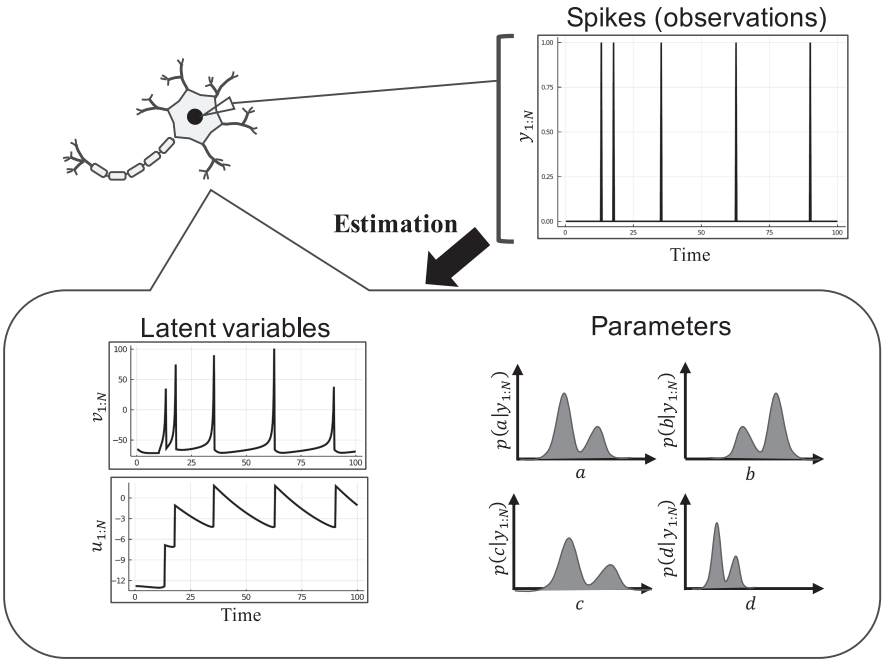


**Fig. 1.** Conceptual diagrams of our study. We propose a method for simultaneously estimating the parameters and the latent variables consisting of the membrane potential $v_{1:N}$ and the membrane recovery variable $u_{1:N}$ in the Izhikevich neuron model from the obtained spikes $y_{1:N}$.

model that expresses various neuronal responses, and realize the precise estimation of neural dynamics from the spike-train data. We also describe the Izhikevich neuron model, formulate the state-space model based on the Izhikevich neuron model, and propose a method for estimating the joint posterior distribution of latent variables and parameters. Moreover, in order to verify the effectiveness of the proposed method, we conduct numerical experiments by using simulated data generated from the Izhikevich neuron model.

## 2. Method

The conceptual diagram of this study is shown in Fig. 1. As shown there, we propose a method that simultaneously estimates the parameters and the latent variables consisting of the membrane potentials and the membrane recovery variables in the Izhikevich neuron model from spike-train data. In this section, we first explain the Izhikevich neuron model that represents the membrane potential activity of neurons. Moreover, we formulate the process of obtaining spikes as the state-space model based on the Izhikevich neuron model, and propose a data-driven method based on the REPGAS for the Izhikevich neuron model to simultaneously estimate the parameters and the latent variables such as the membrane potentials and the membrane recovery variables.

### *2.1 Izhikevich neuron model*

The Izhikevich neuron model is one of the neuronal models that represent the membrane potential activities of neurons.[9,10] Although it is formulated by two relatively simple differential equations for the membrane potential and the membrane recovery variable, it can represent various responses depending on the parameters, and its computational cost is low.

When the membrane potential is expressed as $v$ and the membrane recovery variable is expressed as $u$, the Izhikevich neuron model is represented by the following two differential equations:

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I_{\text{ext}} + \xi_v(t), \tag{1}$$

$$\frac{du}{dt} = a(bv - u) + \xi_u(t), \tag{2}$$

where $I_{\text{ext}}$ is the external input, and $a$ and $b$ are the parameters. In Eqs. (1) and (2), we consider additive white Gaussian noise terms $\xi_v(t)$ and $\xi_u(t)$ for the Izhikevich neuron model [$\langle\xi_v(t)\rangle = \langle\xi_u(t)\rangle = 0$, $\langle\xi_v(t)\xi_v(s)\rangle = \sigma_v^2\delta(t-s)$, $\langle\xi_u(t)\xi_u(s)\rangle = \sigma_u^2\delta(t-s)$, and $\langle\xi_v(t)\xi_u(s)\rangle = 0$, where $\delta(t)$ is the Dirac delta function]. Here, standard deviations of membrane potential and membrane recovery variable are expressed by $\sigma_v$ and $\sigma_u$, respectively. As shown in Fig. 1, the membrane potential $v$ is affected by the membrane recovery variable $u$, and the increase of the membrane potential $v$ is suppressed by the increase of the membrane recovery variable $u$. Moreover, when the membrane recovery variable $u$ decreases, the membrane potential $v$ tends to increase. When the membrane potential $v$ exceeds the threshold value $V_{\text{th}} = 30$, the membrane potential $v$ and the membrane recovery variable $u$ are reset to $c$ and $u + d$, respectively, as follows:

$$v \leftarrow c, \tag{3}$$

$$u \leftarrow u + d, \tag{4}$$

where $c$ and $d$ are also the parameters.

As described above, there are four parameters $\boldsymbol{\theta} = [a, b, c, d]$ in the Izhikevich neuron model, and various responses can be expressed by adjusting these parameters. In Fig. 2 we show the examples of the responses that can be represented by the Izhikevich neuron model. By using different parameters, the various responses, such as the tonic spiking, the phasic spiking, and the mixed mode, are obtained respectively.

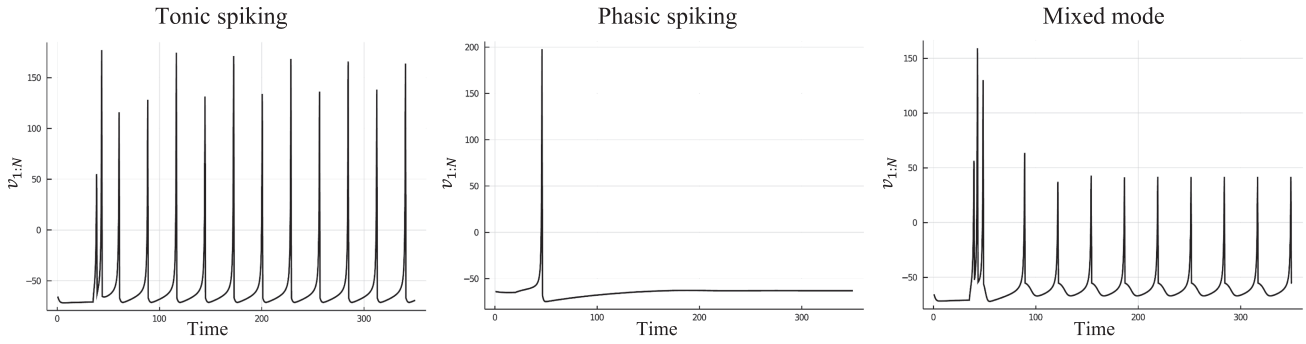


**Fig. 2.** Examples of the responses of the Izhikevich neuron model. In the Izhikevich neuron model, various responses can be represented by adjusting parameters $\boldsymbol{\theta} = [a, b, c, d]$. For example, as examples of three typical responses, tonic spiking (left), phasic spiking (center), and mixed mode (right) are reproduced by $\boldsymbol{\theta} = [0.02, 0.20, -65.0, 6.0]$, $[0.02, 0.25, -65.0, 6.0]$, and $[0.02, 0.20, -55.0, 4.0]$, respectively.

### 2.2 *Replica exchange particle-Gibbs with ancestor sampling method for Izhikevich neuron model*

#### 2.2.1 *State space model for Izhikevich neuron model*

The state space model is a time series model which has been used for time series analysis in various fields (e.g., physics, earth science and brain science) in order to estimate latent variables and forecast observation values.[11–14,16–34] It is represented by two models: a system model that represents the time evolution of latent variables that cannot be observed directly, and an observation model that represents the process of obtaining observations from the latent variables.

In this paper, in order to consider generative process of spike-train data from neuronal dynamics, we discretize the differential equations of the Izhikevich neuron model [Eqs. (1)–(4)] with respect to time, and consider two kinds of descretized latent variables: the membrane potential $v_n$ and the membrane recovery variable $u_n$ at time step $n$. Moreover, we consider that the observation is the number of spikes $y_n$ at each time step $n$.

The system model $p(v_n, u_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta})$, a probabilistic model for latent variables $v_n, u_n$ at time step $n$, is represented as the product of probabilistic models for $v_n$ and $u_n$ given latent variables at the preceding step and parameters $\boldsymbol{\theta} = [a, b, c, d]$ as follows:

$$p(v_n, u_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta}) = p(v_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta}) p(u_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta}). \tag{5}$$

Here, $p(v_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta})$ can be derived by employing the Euler–Maruyama method for Eqs. (1) and (3):

$$p(v_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta}) = \begin{cases} \mathcal{N}(v_n \mid v_{n-1} + \Delta_t(0.04 v_{n-1}^2 + 5 v_{n-1} + 140 - u_{n-1} + I_{\mathrm{ext},n}), \Delta_t \sigma_v^2) & v_{n-1} \le V_{\mathrm{th}} \quad (6) \\ \mathcal{N}(v_n \mid c + \Delta_t(0.04 c^2 + 5c + 140 - u_{n-1} - d + I_{\mathrm{ext},n}), \Delta_t \sigma_v^2) & v_{n-1} > V_{\mathrm{th}}, \quad (7) \end{cases}$$

where $\mathcal{N}(x \mid \mu, \sigma^2)$ is the Gaussian distribution with mean $\mu$ and variance $\sigma^2$, and $\Delta_t$ is the finite length between time steps. Until the membrane potential $v_{n-1}$ exceeds the threshold value $V_{\mathrm{th}}$, the membrane potential $v_n$ obeys the distribution with preceding membrane potential $v_{n-1}$ and other terms expressed by Eq. (6). When it exceeds the threshold value $V_{\mathrm{th}}$, the membrane potential $v_n$ obeys the distribution with reset membrane potential $c$ and other terms expressed by Eq. (7). Similarly, $p(u_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta})$ can be derived based on Eqs. (2) and (4) as follows:

$$p(u_n \mid v_{n-1}, u_{n-1}, \boldsymbol{\theta}) = \begin{cases} \mathcal{N}(u_n \mid u_{n-1} + \Delta_t a(b v_{n-1} - u_{n-1}), \Delta_t \sigma_u^2) & v_{n-1} \le V_{\mathrm{th}} \quad (8) \\ \mathcal{N}(u_n \mid u_{n-1} + d + \Delta_t a(bc - u_{n-1} - d), \Delta_t \sigma_u^2) & v_{n-1} > V_{\mathrm{th}}. \quad (9) \end{cases}$$

Furthermore, we assume that the observation model $p(y_n \mid v_{1:n+k})$, which is the distribution of the number of spikes $y_n$ for a given set of the membrane potentials, $v_{1:n+k}$, in the time steps from 1 to $n+k$, is expressed by the following Poisson distribution:[16]

$$p(y_n \mid v_{1:n+k}) = \frac{1}{y_n!} \exp(y_n \log(\Delta_t \lambda(v_{1:n+k})) - \Delta_t \lambda(v_{1:n+k})), \tag{10}$$

where $\lambda(v_{1:n+k})$ is a function that increases with spiking behavior seen in the membrane potential $v$ around the time step $n$. We assume that the time interval of $\Delta_t$ is sufficiently small and the number of spikes at time step $n$ is either zero or one. The function $\lambda(v_{1:n+k})$ is assumed to be obtained using a sigmoid function with temporal convolution as follows:

$$\lambda(v_{1:n+k}) = \eta \sum_{\tau=1}^{n+k} g(v_\tau) f(\Delta_t(\tau - n)), \tag{11}$$

$$g(v) = \frac{1}{1 + \exp(-\beta(v - V_g))}, \tag{12}$$

$$f(\tau) = \begin{cases} p^{-\tau} & \tau \le 0 \\ q^{\tau} & \tau > 0, \end{cases} \tag{13}$$

where $V_g$ is a constant representing a firing threshold, and $\eta$, $\beta$, $p$, and $q$ are positive constants.

#### 2.2.2 *Replica exchange particle-Gibbs with ancestor sampling method*

We propose a method for simultaneously estimating the membrane potentials $v_{1:N}$, the membrane recovery variables $u_{1:N}$, and the parameters $\boldsymbol{\theta} = [a, b, c, d]$ in the Izhikevich

neuron model from spikes $y_{1:N}$ by employing the REPGAS method.[34] The REPGAS method is one of the PMCMC methods, and can be used to obtain samples from the joint posterior distribution $p(v_{1:N}, u_{1:N}, \boldsymbol{\theta} \mid y_{1:N})$ of the latent variables, $v_{1:N}$ and $u_{1:N}$, and the parameters $\boldsymbol{\theta}$. In our study, by collecting the samples obtained by the REPGAS method, we estimate the joint posterior distribution $p(v_{1:N}, u_{1:N}, \boldsymbol{\theta} \mid y_{1:N})$.

In the REPGAS method, we introduce $R$ different temperatures $\boldsymbol{T} = [T^1, T^2, \ldots, T^R]$ as extension variables and consider the following extended joint posterior distribution:

$$\pi_{\mathrm{EX}}(\{v_{1:N}\}, \{u_{1:N}\}, \{\boldsymbol{\theta}\} \mid y_{1:N}) = \prod_{r=1}^{R} \pi_{T^r}(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N}), \tag{14}$$

where the membrane potentials $\{v_{1:N}\}$, the membrane recovery variables $\{u_{1:N}\}$, and the parameters $\{\boldsymbol{\theta}\}$ in all temperatures $\boldsymbol{T}$ are represented as $\{v_{1:N}\} = \{v^1_{1:N}, \ldots, v^R_{1:N}\}$, $\{u_{1:N}\} = \{u^1_{1:N}, \ldots, u^R_{1:N}\}$, and $\{\boldsymbol{\theta}\} = \{\boldsymbol{\theta}^1, \ldots, \boldsymbol{\theta}^R\}$, respectively. Furthermore, the joint posterior distribution at each temperature $\pi_{T^r}(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N})$ is represented as follows:

$$\pi_{T^r}(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N}) = \frac{1}{Z(T^r)} p(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N})^{\frac{1}{T^r}}, \tag{15}$$

where $Z(T^r)$ represents the partition function, and $p(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N})$ is represented as follows:

$$p(v^r_{1:N}, u^r_{1:N}, \boldsymbol{\theta}^r \mid y_{1:N}) = \frac{p(y_{1:N} \mid v^r_{1:N}) p(v^r_{1:N}, u^r_{1:N} \mid \boldsymbol{\theta}^r) p(\boldsymbol{\theta}^r)}{p(y_{1:N})}, \tag{16}$$

where $p(y_{1:N} \mid v^r_{1:N})$ and $p(v^r_{1:N}, u^r_{1:N} \mid \boldsymbol{\theta}^r)$ are evaluated by using the observation model [Eq. (10)] and the system model [Eq. (5)] for all time steps, respectively. Here, $p(\boldsymbol{\theta}^r)$ is the prior distribution of the parameters $\boldsymbol{\theta}^r$, and $p(y_{1:N})$ is the marginal likelihood.

We obtain samples of the parameters $\boldsymbol{\theta}^r$ and the latent variables consisting of the membrane potentials $v^r_{1:N}$ and the membrane recovery variables $u^r_{1:N}$ alternately for each temperature according to Eq. (15). The $l$-th samples of latent variables, $v^r_{1:N}[l]$ and $u^r_{1:N}[l]$, are obtained from $p(v^r_{1:N}, u^r_{1:N} \mid v^r_{1:N}[l-1], u^r_{1:N}[l-1], y_{1:N}, \boldsymbol{\theta}^r[l-1])$ with the conditional SMC with ancestor sampling. In the conditional SMC with ancestor sampling, the distribution of latent variables is approximated by particles, $\{v^{(1)}_{1:N}, v^{(2)}_{1:N}, \ldots, v^{(M)}_{1:N}\}$ and $\{u^{(1)}_{1:N}, u^{(2)}_{1:N}, \ldots, u^{(M)}_{1:N}\}$, as follows:

$$p(v_{1:N}, u_{1:N} \mid v^r_{1:N}[l-1], u^r_{1:N}[l-1], y_{1:N}, \boldsymbol{\theta}^r[l-1]) \simeq \frac{1}{M} \sum_{i=1}^{M} \delta(v_{1:N} - v^{(i)}_{1:N}) \delta(u_{1:N} - u^{(i)}_{1:N}), \tag{17}$$

where $v^{(i)}_{1:N}$ and $u^{(i)}_{1:N}$ are the latent variables of $i$-th particle, $M$ is the number of particles. To obtain particles, at the time step $n$, the indices of ancestor particles $\{A^{(1)}_{n-1}, A^{(2)}_{n-1}, \ldots, A^{(M-1)}_{n-1}\}$ at the previous time step $n-1$, are sampled based on the normalized weights $\{W^{(1)}_{n-1}, W^{(2)}_{n-1}, \ldots, W^{(M)}_{n-1}\}$ obtained as follows:

$$W^{(i)}_{n-1} = \frac{w^{(i)}_{n-1}}{\sum_{j=1}^{M} w^{(j)}_{n-1}}, \tag{18}$$

$$w^{(i)}_{n-1} = p(y_{n-1} \mid v^{(i)}_{1:n+k-1}), \tag{19}$$

where $w^{(i)}_{n-1}$ is the unnormalized weight for $i$-th particle. Here, the likelihood of the $i$-th particle, $p(y_{n-1} \mid v^{(i)}_{1:n+k-1})$, is calculated using the observation model [Eq. (10)] with observation data $y_{n-1}$ and membrane potential of $i$-th particle $v^{(i)}_{1:n+k-1}$. Latent variables at the time step $n$, $v_n$, and $u_n$, are sampled from the system model $p(v_n, u_n \mid v^{(A^{(i)}_{n-1})}_{n-1}, u^{(A^{(i)}_{n-1})}_{n-1}, \boldsymbol{\theta}^r[l-1])$. The particles are set to be $v^{(i)}_{1:n} \leftarrow \{v^{(A^{(i)}_{n-1})}_{1:n-1}, v^{(i)}_n\}$ and $u^{(i)}_{1:n} \leftarrow \{u^{(A^{(i)}_{n-1})}_{1:n-1}, u^{(i)}_n\}$ for particle numbers $i \in \{1, 2, \ldots, M-1\}$, while the $M$-th particle is set to be the previous sample $v^{(M)}_{1:n} \leftarrow \{v^{(A^{(M)}_{n-1})}_{1:n-1}, v^r_n[l-1]\}$ and $u^{(M)}_{1:n} \leftarrow \{u^{(A^{(M)}_{n-1})}_{1:n-1}, u^r_n[l-1]\}$. Here, the index of ancestor particle $A^{(M)}_{n-1}$ is sampled based on the normalized weights $\{\hat{W}^{(1)}_{n-1}, \hat{W}^{(2)}_{n-1}, \ldots, \hat{W}^{(M)}_{n-1}\}$ calculated as follows:

$$\hat{W}^{(i)}_{n-1} = \frac{\hat{w}^{(i)}_{n-1}}{\sum_{j=1}^{M} \hat{w}^{(j)}_{n-1}}, \tag{20}$$

$$\hat{w}^{(i)}_{n-1} = W^{(i)}_{n-1} p(v^r_n[l-1], u^r_n[l-1] \mid v^{(i)}_{n-1}, u^{(i)}_{n-1}, \boldsymbol{\theta}^r[l-1]), \tag{21}$$

where $\hat{w}^{(i)}_{n-1}$ is the unnormalized weight for sampling the index of ancestor particle $A^{(M)}_{n-1}$. Here, $p(v^r_n[l-1], u^r_n[l-1] \mid v^{(i)}_{n-1}, u^{(i)}_{n-1}, \boldsymbol{\theta}^r[l-1])$ is calculated by using the system model [Eq. (5)] with the following variables and parameters: the latent variables of previous sample at time step $n$, $v^r_n[l-1]$ and $u^r_n[l-1]$, the latent variables of $i$-th particle at time step $n-1$, $v^{(i)}_{n-1}$, and $u^{(i)}_{n-1}$, and the parameters of previous sample $\boldsymbol{\theta}^r[l-1]$. We iterate the above flow from time step 1 to $N$ and the $l$-th sample of the latent variables, $v^r_{1:N}[l]$ and $u^r_{1:N}[l]$, is obtained based on normalized weights $\{W^{(1)}_N, W^{(2)}_N, \ldots, W^{(M)}_N\}$. The $l$-th sample of the parameters $\boldsymbol{\theta}^r[l]$ is obtained from $p(\boldsymbol{\theta} \mid v^r_{1:N}[l], u^r_{1:N}[l], y_{1:N})$ with the Metropolis method.[24,41]

In REPGAS, we obtain samples at each temperature as described above, and exchange samples between temperatures $T^r$ and $T^{r+1}$ according to the following exchange probability:

$$p_{\mathrm{EX}} = \min(1, R_{\mathrm{EX}}), \tag{22}$$

$$R_{\mathrm{EX}} = \frac{\pi_{\mathrm{EX}}(\{v^*_{1:N}\}, \{u^*_{1:N}\}, \{\boldsymbol{\theta}^*\} \mid y_{1:N})}{\pi_{\mathrm{EX}}(\{v_{1:N}\}, \{u_{1:N}\}, \{\boldsymbol{\theta}\} \mid y_{1:N})}, \tag{23}$$

where $\{v^*_{1:N}\}$, $\{u^*_{1:N}\}$, and $\{\boldsymbol{\theta}^*\}$ are expressed as follows:

$$\{v^*_{1:N}\} = \{v^1_{1:N}, \ldots, v^{r+1}_{1:N}, v^r_{1:N}, \ldots, v^R_{1:N}\}, \tag{24}$$

$$\{u^*_{1:N}\} = \{u^1_{1:N}, \ldots, u^{r+1}_{1:N}, u^r_{1:N}, \ldots, u^R_{1:N}\}, \tag{25}$$

$$\{\boldsymbol{\theta}^*\} = \{\boldsymbol{\theta}^1, \ldots, \boldsymbol{\theta}^{r+1}, \boldsymbol{\theta}^r, \ldots, \boldsymbol{\theta}^R\}. \tag{26}$$

We summarize the algorithm of the REPGAS method for Izhikevich neuron model in Algorithm 1. The sampling efficiency of PG is improved by passing through a high temperature state in the replica exchange method. Moreover, it can prevent increasing the calculation time because sampling at each temperature can be parallelized.

## 3. Results

In this section, we verify the effectiveness of the proposed method. First, we estimate the joint posterior distribution $p(v_{1:N}, u_{1:N}, \boldsymbol{\theta} \mid y_{1:N})$ of the parameters $\boldsymbol{\theta}$ and the latent variables consisting of the membrane potentials $v_{1:N}$ and the membrane recovery variables $u_{1:N}$ by employing the

**Algorithm 1** REPGAS method for Izhikevich neuron model

1: initialize the membrane potentials $\{v_{1:N}\}[0]$ and the membrane recovery variables $\{u_{1:N}\}[0]$
2: initialize the samples of the parameters $\{\boldsymbol{\theta}\}[0]$
3: **for** $l = 1, \ldots, L$ **do**
4: **for** $r = 1, \ldots, R$ **do**
5: sample the membrane potentials $v^r_{1:N}[l]$ and the membrane recovery variables $u^r_{1:N}[l]$ from the distribution in Eq. (17) by employing the conditional SMC method
6: sample the parameters $\boldsymbol{\theta}^r[l]$ from the distribution $p(\boldsymbol{\theta} \mid v^r_{1:N}[l], u^r_{1:N}[l], y_{1:N})$ by employing the Metropolis method
7: **end for**
8: choose replica numbers $r$ and $r+1$ for exchanging
9: calculate $p_{\mathrm{EX}}$ with Eq. (22)
10: draw a uniform random number $\alpha_{\mathrm{EX}}$ with range $[0, 1)$
11: **if** $\alpha_{\mathrm{EX}} \leq p_{\mathrm{EX}}$ **then**
12: exchange replicas $(\{v_{1:N}\}[l], \{u_{1:N}\}[l], \{\boldsymbol{\theta}\}[l]) \leftarrow (\{v^*_{1:N}\}[l], \{u^*_{1:N}\}[l], \{\boldsymbol{\theta}^*\}[l])$
13: **end if**
14: **end for**

**Table I.** True parameters of the Izhikevich neuron model for the experiments.[10)]

| Model | $a$ | $b$ | $c$ | $d$ |
|---|---|---|---|---|
| (i) Tonic spiking | 0.02 | 0.20 | −65.0 | 6.0 |
| (ii) Phasic spiking | 0.02 | 0.25 | −65.0 | 6.0 |
| (iii) Mixed mode | 0.02 | 0.20 | −55.0 | 4.0 |
| (iv) Rebound spike | 0.03 | 0.25 | −60.0 | 4.0 |

proposed method for the simulation data generated from the Izhikevich neuron model. Next, the estimation results of the proposed method and other methods are compared for some typical response characteristic parameters. Finally, the reproducibility of the response is verified with the inputs not used for estimation of parameters and the parameters estimated by each method.

In this paper, we use the simulated data generated with the four parameter sets (i) tonic spiking, (ii) phasic spiking, (iii) mixed mode, and (iv) rebound spike shown in Table I. The variances of the membrane potentials $v_{1:N}$ and the membrane recovery variables $u_{1:N}$ are $\sigma_v^2 = 0.25$ and $\sigma_u^2 = 10^{-4}$, respectively. As an example of the data used, the data generated with the parameters of (i) tonic spiking is shown in Fig. 3, where the true membrane potentials $v_{1:N}$, the true membrane recovery variables $u_{1:N}$, the spikes $y_{1:N}$, and the input currents $I_{\mathrm{ext},1:N}$ are shown in order from the top. The horizontal axes represent the time, and the vertical axes represent the value of each variable. The latent variables, $v_{1:N}$ and $u_{1:N}$, and the parameters $\boldsymbol{\theta}$ are estimated from spikes $y_{1:N}$ obtained by applying the same input currents $I_{\mathrm{ext},1:N}$ to other parameter sets. In the proposed method, the number of particles $M$ is 50, the number of samples $L$ is $3 \times 10^5$, the number of burn-in samples $L_{\text{burn-in}}$ is $1.5 \times 10^5$, the number of replicas $R$ is 64, and the temperatures $\boldsymbol{T}$ are set as $\boldsymbol{T} = [1.0, 1.1, 1.1^2, \ldots, 1.1^{R-1}]$. Moreover, we assume that the prior distribution $p(\boldsymbol{\theta})$ is a uniform distribution. In this paper, we focus on estimating parameters $\boldsymbol{\theta} = [a, b, c, d]$ and assume that the variances $\{\sigma_v^2, \sigma_u^2\}$ of the membrane potentials $v_{1:N}$ and the membrane recovery variables $u_{1:N}$ are known. Furthermore, for all estimation results, the parameter set of (i) tonic spiking is used as the initial value, and the hyper parameters for the observation model are $\eta = 1.02$, $\beta = 0.28$, $V_g = -19.5$, $p = 0.23$, and $q = 0.05$.

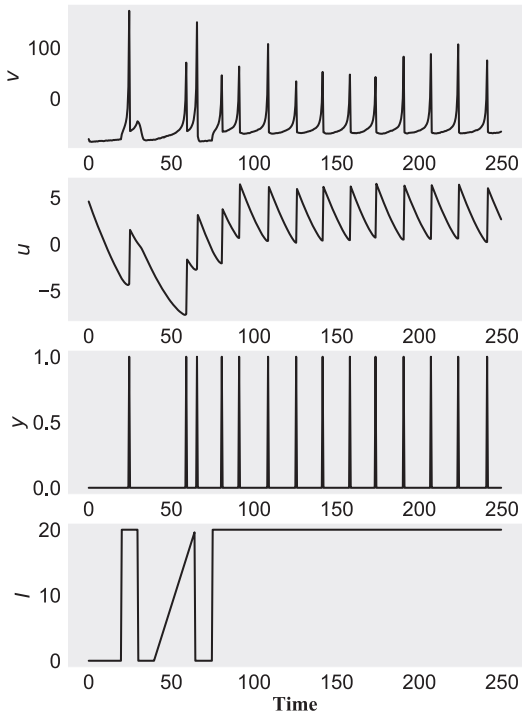


**Fig. 3.** Generated data with the parameters of (i) tonic spiking. From the top, they are the graphs of the true membrane potentials $v_{1:N}$, the true membrane recovery variable $u_{1:N}$, the spikes $y_{1:N}$, and the input currents $I_{\mathrm{ext},1:N}$. The horizontal axes show the time and the vertical axes show the value of each variable. All the data are generated by applying the same input currents $I_{\mathrm{ext},1:N}$ for each parameter set.

Figures 4 and 5 are the estimated distributions of the parameters $\boldsymbol{\theta} = [a, b, c, d]$ of (iii) mixed mode and (iv) rebound spike by using the proposed method. As shown in Fig. 4, even though true values of $c$ and $d$ ($c = -55.0$, $d = 4.0$) are far from initial values ($c = -65.0$, $d = 6.0$), the true values of (iii) mixed mode are found to be estimated appropriately. Also in Fig. 5, although all the true parameters ($a = 0.03$, $b = 0.25$, $c = -60.0$, $d = 4.0$) are different from the initial values ($a = 0.02$, $b = 0.20$, $c = -65.0$, $d = 6.0$), all the parameters show high probability densities around the true values of (iv) rebound spike, and it can be verified that the estimations can be performed appropriately. Moreover, since not only the global optimum but also the local optimum can be found simultaneously, it can be verified that a wide range can be searched. Figures 6 and 7 are the estimated results of the latent variables such as the membrane potentials $v_{1:N}$ and the membrane recovery variables $u_{1:N}$. There the horizontal axes represent the time, and the vertical axes represent the value of each latent variable. In each graph, the solid lines represent the true values and the filled areas represent the 95% confidence intervals of the estimated distributions. In both figures, the complex response of the membrane potential can be properly captured, and it can be verified that the estimations are properly performed.

Next, we show in the Table II the estimated results of all parameter sets. As results estimated by other methods, we show the results estimated by the SMC method with the SOSSM, the method to estimate the parameters in the SMC method by considering the parameters as a part of latent variables,[16,20)] and results estimated by the SMC method with the EM algorithm, a point estimation method that sequen-

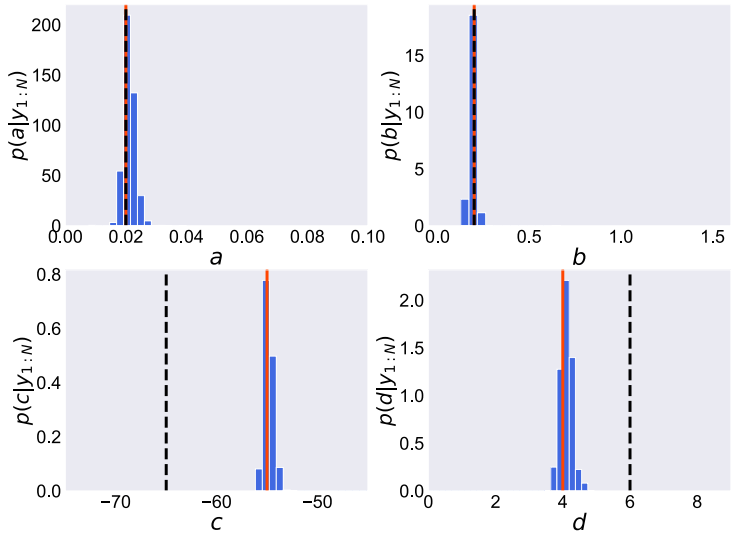


**Fig. 4.** (Color online) Estimated result of parameters of (iii) mixed mode by the REPGAS method. The horizontal axes represent the value of each parameter, the vertical axes represent the probability densities, the red solid lines represent the true values, the black dashed lines represent the initial values, and the blue histograms represent the estimated distributions.

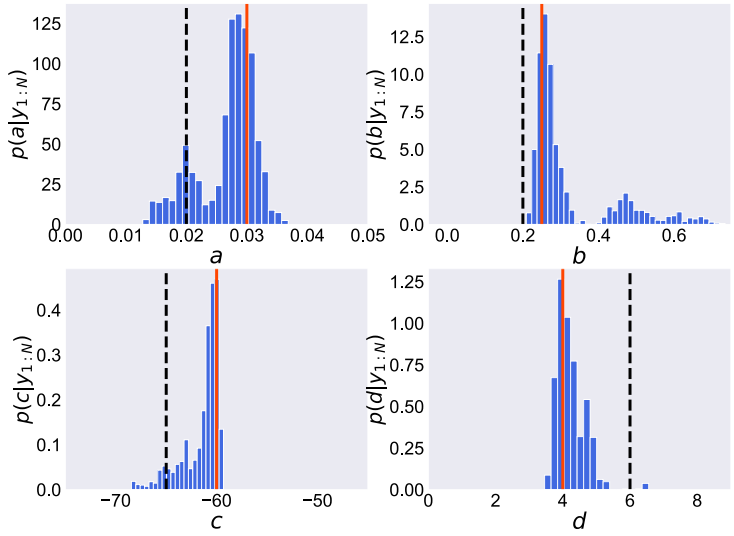


**Fig. 5.** (Color online) Estimated result of parameters of (iv) rebound spike by the REPGAS method. See also the captions for Fig. 4.

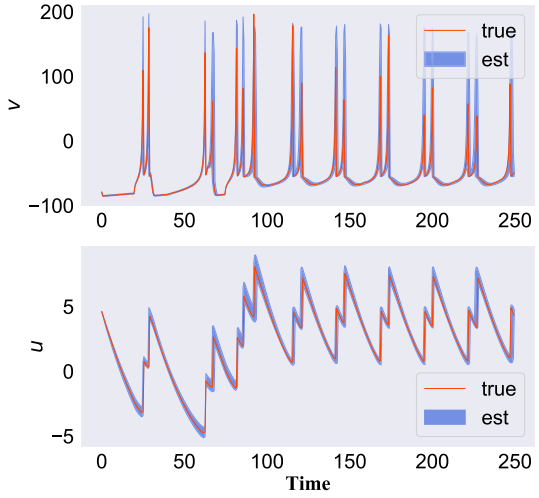


**Fig. 6.** (Color online) Estimated result of latent variables of (iii) mixed mode by the REPGAS method. The horizontal axes represent the time, the vertical axes represent the value of each latent variable, the red solid lines are the true values, and the blue filled areas represent the 95% confidence intervals of the estimated distributions.

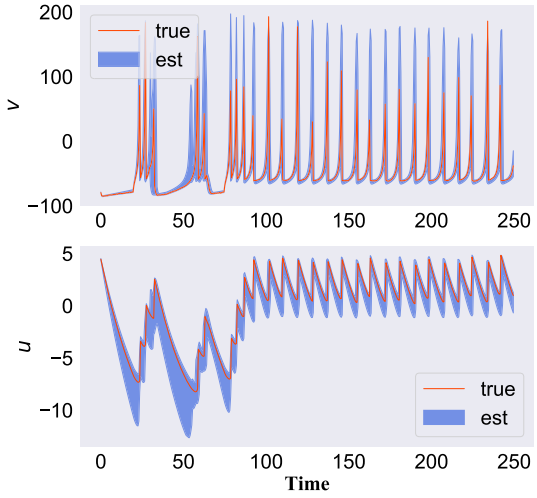


**Fig. 7.** (Color online) Estimated result of latent variables of (iv) rebound spike by the REPGAS method. See also the captions for Fig. 6.

**Table II.** Estimated results of parameters in the Izhikevich neuron model.

| Model | Parameter | True | SMC+SOSSM | | SMC+EM | REPGAS | |
|---|---|---|---|---|---|---|---|
| | | | Mode | Std | | Mode | Std |
| (i) Tonic spiking | $a$ | 0.0200 | 0.0251 | 0.0081 | 0.0216 | **0.0207** | 0.0068 |
| | $b$ | 0.200 | 0.151 | 0.289 | 0.181 | **0.193** | 0.389 |
| | $c$ | −65.00 | −60.04 | 4.12 | −63.70 | **−64.13** | 6.20 |
| | $d$ | 6.00 | **5.94** | 1.15 | 5.92 | **5.94** | 1.05 |
| (ii) Phasic spiking | $a$ | 0.0200 | 0.0222 | 0.0039 | 0.0255 | **0.0202** | 0.0058 |
| | $b$ | 0.250 | 0.224 | 0.168 | 0.146 | **0.250** | 0.153 |
| | $c$ | −65.00 | −67.10 | 1.36 | −87.46 | **−65.39** | 2.63 |
| | $d$ | 6.00 | 6.04 | 0.27 | 6.08 | **6.00** | 0.69 |
| (iii) Mixed mode | $a$ | 0.0200 | 0.0170 | 0.00002 | 0.0119 | **0.0202** | 0.0019 |
| | $b$ | 0.200 | 0.222 | 0.0007 | 0.336 | **0.201** | 0.021 |
| | $c$ | −55.00 | −55.33 | 0.01 | −73.31 | **−54.98** | 0.53 |
| | $d$ | 4.00 | 3.62 | 0.01 | 5.79 | **4.01** | 0.20 |
| (iv) Rebound spike | $a$ | 0.0300 | 0.0387 | 0.0020 | 0.0154 | **0.0299** | 0.0048 |
| | $b$ | 0.250 | 0.224 | 0.011 | 0.272 | **0.252** | 0.115 |
| | $c$ | −60.00 | −58.72 | 0.59 | −87.50 | **−60.00** | 1.87 |
| | $d$ | 4.00 | 4.62 | 0.22 | 6.00 | **4.00** | 0.43 |

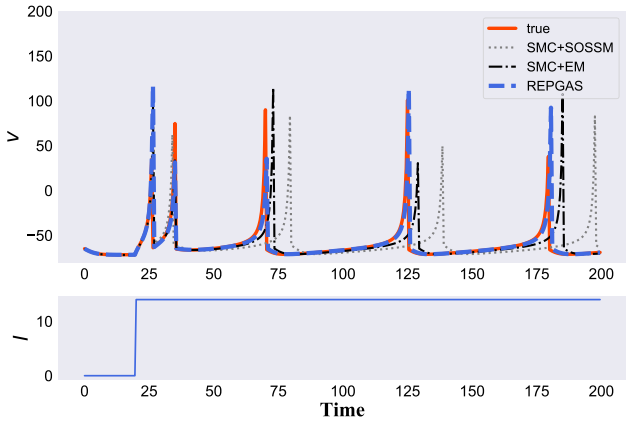


**Fig. 8.** (Color online) Comparison of reproduction results of (i) tonic spiking response. The upper graph shows the membrane potentials $v_{1:N}$, the lower graph shows the input currents $I_{\mathrm{ext},1:N}$, the horizontal axes show the time, and the vertical axes show the value of each variable. In the upper graph, the response obtained when using the true parameters (red solid line), the responses obtained when using the parameters estimated by the REPGAS method (blue dashed line), the responses obtained when using the parameters estimated by the SMC method with the EM algorithm (black dashed-dotted line), and the responses obtained when using the parameters estimated by the SMC method with the SOSSM (gray dotted line) are shown.

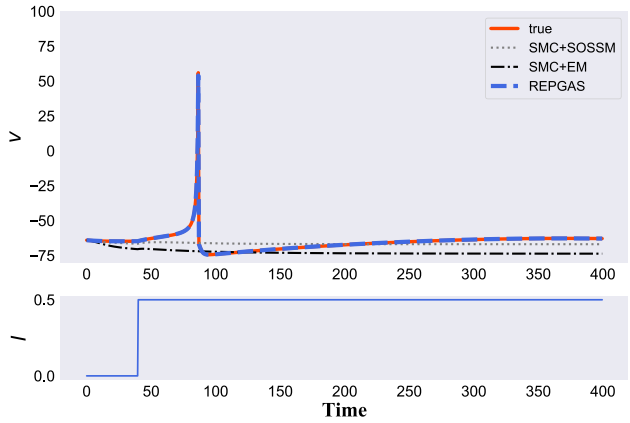


**Fig. 9.** (Color online) Comparison of reproduction results of (ii) phasic spiking response. See also the captions for Fig. 8.

tially updates the parameters so that the likelihood increase.[11–14,31] In the SMC method with the SOSSM, the number of particles $M_{\mathrm{SOSSM}}$ is $5 \times 10^5$, and the parameters of the initial particles are generated as follows using a uniform distribution:

$$a \sim U(0, 0.5), \tag{27}$$

$$b \sim U(-1.5, 1.0), \tag{28}$$

$$c \sim U(-70, -50), \tag{29}$$

$$d \sim U(3, 10). \tag{30}$$

Here, $U(x, y)$ is a uniform distribution between $x$ and $y$. In the SMC method with the EM algorithm, the number of particles $M_{\mathrm{EM}}$ is $10^3$, the number of iterations $L_{\mathrm{EM}}$ is $10^4$, and the initial values of parameters are the parameters of (i) tonic spiking as in the proposed method. In the proposed method and the SMC method with the SOSSM, the mode values of the estimated distributions are used as the estimated results. One can see from the results in Table II, that values close to the true values can be estimated by the SMC method with the SOSSM in some models. However, it is considered that the particles closer to the true values have been lost due to the degeneracy of the SMC method since the standard deviations of the result of (iii) mixed mode are very small values. Regarding the results of the SMC method with the EM algorithm, compared to the result of (i) tonic spiking, which starts the estimation from the true values, the estimation results of the other parameter sets are poor. Since this method is a point estimation method, it is considered that the global optimum could not be estimated without getting out of the local optimum. In our proposed method, it can be verified that the estimated values are closest to the true values in all parameter sets.

Finally, in Figs. 8, 9, 10, and 11, we show results when comparing the reproducibilities of the responses to the new inputs with the parameter sets estimated by each method for (i) tonic spiking, (ii) phasic spiking, (iii) mixed mode, and (iv) rebound spike, respectively. In each figure, the upper graphs show the reproduction results of the membrane potentials $v_{1:N}$, the lower graphs show the input currents $I_{\mathrm{ext},1:N}$, the vertical axes show the value of each variable, and

**Table III.** Reproducibility comparison results for new inputs.

| | Model | True | SMC+SOSSM | SMC+EM | REPGAS |
|---|---|---|---|---|---|
| RMSE | (i) Tonic spiking | | 25.76 | 23.74 | **18.09** |
| | (ii) Phasic spiking | | 7.04 | 10.21 | **0.09** |
| | (iii) Mixed mode | | 22.49 | 24.54 | **10.57** |
| | (iv) Rebound spike | | 7.43 | 10.62 | **7.11** |
| Number of spikes | (i) Tonic spiking | 5 | **5** | **5** | **5** |
| | (ii) Phasic spiking | 1 | 0 | 0 | **1** |
| | (iii) Mixed mode | 6 | 8 | **6** | **6** |
| | (iv) Rebound spike | 1 | 0 | 2 | **1** |
| Average deviation time of the spike timings | (i) Tonic spiking | | +8.1 | +2.6 | **+0.5** |
| | (ii) Phasic spiking | | — | — | **0.0** |
| | (iii) Mixed mode | | −19.67 | 17.58 | **−0.5** |
| | (iv) Rebound spike | | — | −5.0 | **−3.0** |

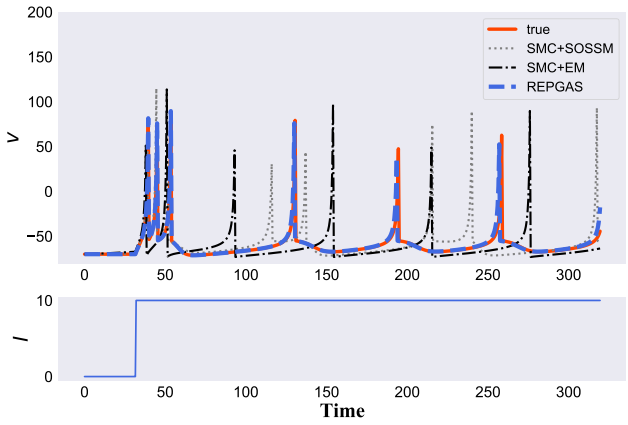


**Fig. 10.** (Color online) Comparison of reproduction results of (iii) mixed mode response. See also the captions for Fig. 8.

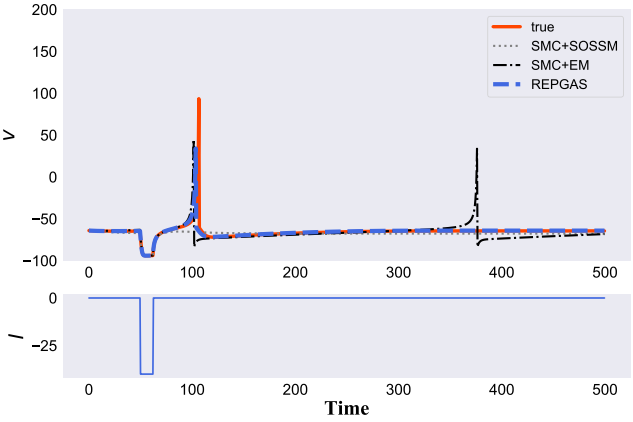


**Fig. 11.** (Color online) Comparison of reproduction results of (iv) rebound spike response. See also the captions for Fig. 8.

the horizontal axes show the time. In the upper graphs, the solid lines show the responses obtained when using the true parameters, and the dotted lines, the dashed-dotted lines, and the dashed lines show the responses obtained when using the parameters estimated by the SMC method with the SOSSM, the SMC method with the EM algorithm, and the REPGAS method, respectively. In all figures, it can be verified that the proposed method can output spikes at timings closer to the simulation results with true parameters than the results of the other methods. It is also verified in Figs. 9 and 11 that the number of spikes is correct only in the results of the proposed method. Table III shows the quantitative comparison results of each method. There we compare the root mean square error (RMSE), the number of spikes, and the average deviation time of the spike timings when the membrane potentials are reproduced by each parameter. In the average deviation time of the spike timings, "—" is displayed if no spikes can be output and the calculation cannot be performed. It can be verified that our REPGAS method shows the best results for all results. The above results confirm that Izhikevich neuron model parameters that can reproduce actual responses can be estimated from the spike-train data by using the proposed method.

## 4. Conclusion

In this paper, we proposed the method to estimate the parameter and the latent variables consisting of the membrane potentials and the membrane recovery variables of the Izhikevich neuron model from only spike-train data based on the REPGAS method. In the proposed method, the process of obtaining spikes is formulated as the state space model based on the Izhikevich neuron model, and the latent variables and the parameters are estimated simultaneously by employing the REPGAS method. Moreover, we verified that the latent variables and the parameters of the Izhikevich neuron model can be estimated simultaneously by using the proposed method for simulated data generated from the Izhikevich neuron model with several parameter sets. Furthermore, it was also shown that the proposed method can estimate parameters closer to the true values than the SMC method with the SOSSM and the SMC method with the EM algorithm, and that the responses to new inputs are more reproducible.

**Acknowledgments** This work is partially supported by Grants-in-Aid for Scientific Research for Innovative Areas "Initiative for High-Dimensional Data driven Science through Deepening of Sparse Modeling" (JSPS KAKENHI Grant No. JP25120010) and for Scientific Research (B) (JSPS KAKENHI Grant Nos. JP17H02923, JP19H04125, JP21H3509), and a Fund for the Promotion of Joint International Research (Fostering Joint International Research) (JSPS KAKENHI Grant No. JP15KK0010) from the Ministry of Education, Culture, Sports, Science and Technology of Japan, and CREST (Nos. JPMJCR1755, JPMJCR1861, JPMJCR1914), Japan Science and Technology Agency, Japan.

*omori@eedept.kobe-u.ac.jp

1) A. L. Hodgkin and A. F. Huxley, J. Physiol. **117**, 500 (1952).
2) R. Fitzhugh, Biophys. J. **1**, 445 (1961).
3) C. Morris and H. Lecar, Biophys. J. **35**, 193 (1981).

4) R. M. Rose and J. L. Hindmarsh, Proc. R. Soc. London, Ser. B **237**, 267 (1989).
5) H. R. Wilson, J. Theor. Biol. **200**, 375 (1999).
6) G. D. Smith, C. L. Cox, S. M. Sherman, and J. Rinzel, J. Neurophysiol. **83**, 588 (2000).
7) P. E. Latham, B. J. Richmond, P. G. Nelson, and S. Nirenberg, J. Neurophysiol. **83**, 808 (2000).
8) E. M. Izhikevich, Neural Networks **14**, 883 (2001).
9) E. M. Izhikevich, IEEE Trans. Neural Networks **14**, 1569 (2003).
10) E. M. Izhikevich, IEEE Trans. Neural Networks **15**, 1063 (2004).
11) J. T. Vogelstein, B. O. Watson, A. M. Packer, R. Yuste, B. Jedynak, and L. Paninski, Biophys. J. **97**, 636 (2009).
12) J. T. Vogelstein, A. M. Packer, T. A. Machado, T. Sippy, B. Babadi, R. Yuste, and L. Paninski, J. Neurophysiol. **104**, 3691 (2010).
13) T. Tsunoda, T. Omori, H. Miyakawa, M. Okada, and T. Aonishi, J. Phys. Soc. Jpn. **79**, 124801 (2010).
14) L. Paninski, M. Vidne, B. DePasquale, and D. G. Ferreira, J. Comput. Neurosci. **33**, 1 (2012).
15) Y. Dong, S. Mihalas, A. Russell, R. Etienne-Cummings, and E. Niebur, Neural Comput. **23**, 2833 (2011).
16) L. Meng, M. A. Kramer, and U. T. Eden, J. Neural Eng. **8**, 065006 (2011).
17) M. L. Andrade Netto, L. Gemenao, and M. J. Mendes, IFAC Proc. Vol. **11**, 2123 (1978).
18) A. Doucet, S. Godsill, and C. Andrieu, Stat. Comput. **10**, 197 (2000).
19) Z. Ghahramani and G. E. Hinton, University of Toronto, Technical Report CRG-TR-96-2 (1996).
20) G. Kitagawa, J. Am. Stat. Assoc. **93**, 1203 (1998).
21) R. Meyer and N. Christensen, Phys. Rev. E **65**, 016206 (2001).
22) A. Doucet, N. de Freitas, and N. Gordon, *Sequential Monte Carlo Methods in Practice* (Springer, New York, 2001).
23) R. J. Hyndman, A. B. Koehler, R. D. Snyder, and S. Grose, Int. J. Forecasting **18**, 439 (2002).
24) C. M. Bishop, *Pattern Recognition and Machine Learning* (Springer, Heidelberg, 2006).
25) C. Andrieu, A. Doucet, and R. Holenstein, J. R. Stat. Soc., Ser. B **72**, 269 (2010).
26) R. D. Snyder, J. K. Ord, A. B. Koehler, K. R. McLaren, and A. N. Beaumont, Int. J. Forecasting **33**, 502 (2017).
27) F. Lindsten, T. Schön, and M. I. Jordan, Adv. Neural Inf. Process. Syst. **25**, 2600 (2012).
28) S. Henriksen, A. Wills, T. B. Schön, and B. Ninness, IFAC Proc. Vol. **45**, 1143 (2012).
29) R. Frigola, F. Lindsten, T. B. Schön, and C. E. Rasmussen, Adv. Neural Inf. Process. Syst. **26**, 3181 (2013).
30) F. Lindsten, M. I. Jordan, and T. B. Schön, J. Mach. Learn. Res. **15**, 2145 (2014).
31) T. Omori, T. Kuwatani, A. Okamoto, and K. Hukushima, Phys. Rev. E **94**, 033305 (2016).
32) T. Omori, T. Sekiguchi, and M. Okada, J. Phys. Soc. Jpn. **86**, 084802 (2017).
33) S. S. Rangapuram, M. W. Seeger, J. Gasthaus, L. Stella, Y. Wang, and T. Januschowski, Adv. Neural Inf. Process. Syst. **31**, 7796 (2018).
34) H. Inoue, K. Hukushima, and T. Omori, J. Phys. Soc. Jpn. **89**, 104801 (2020).
35) C. F. J. Wu, Ann. Stat. **11**, 95 (1983).
36) G. J. McLachlan and T. Krishnan, *The EM Algorithm and Its Extensions* (Wiley, New York, 1997).
37) S. Geman and D. Geman, IEEE Trans. Pattern Anal. Mach. Intell. **PAMI-6**, 721 (1984).
38) K. Hukushima and K. Nemoto, J. Phys. Soc. Jpn. **65**, 1604 (1996).
39) R. Urano and Y. Okamoto, Comput. Phys. Commun. **196**, 380 (2015).
40) K. Motonaka and S. Miyoshi, Neural Networks **118**, 159 (2019).
41) N. Metropolis, A. W. Rosenbluth, M. N. Rosenbluth, and A. H. Teller, J. Chem. Phys. **21**, 1087 (1953).